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Published in:
Vision Research

DOI:
10.1016/0042-6989(93)90237-Q

Publication date:
1993

Vision Res. Vol. 33, No. 8, pp. 1011–1017, 1993
Printed in Great Britain.

0042-6989/93 $6.00 + 0.00

Research Note

Simple Exponential Functions Describing the Absorbance Bands of Visual Pigment Spectra

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Received 3 September 1991; in revised form 17 November 1992

Literature data for visual pigment spectra are formally treated by assuming that the spectra consist of a summation of absorbance bands, that the shape of the bands is invariant according to the Mansfield–MacNichol transform and that this shape is described by simple exponential functions. A new template for constructing visual pigment spectra from peak wavelengths is derived.

Visual pigment Nomogram Absorbance band Spectral shape Template

INTRODUCTION

In vision research, the precise shape of the absorbance spectrum of a visual pigment is a recurrent question. In numerous optical and physiological studies, knowledge of the spectral shape has proved to be crucial (e.g. Wyszecki & Stiles, 1982). Ideally, the shape of visual pigment spectra is predicted by theory, but so far, and probably for some time to go, only qualitative, heuristic methods are to our disposal. Here we review the different approaches attempted and compare their validity. We thus hope to provide useful tools for various branches of vision research.

History of visual pigment templates

On the basis of the absorbance spectra known at the time, Dartnall (1953) proposed that the normalized absorbance spectrum of any vitamin A_1-based visual pigment, when plotted on a frequency scale, has a standard shape, independent of the absorbance peak wavelength, λ_{max}. The accordingly devised Dartnall nomogram, from which the complete spectrum could be derived for any given λ_{max}, has been widely used in predicting the peak wavelength together with the shape of a visual pigment spectrum, especially when only a limited set of experimental data was available.

The visual pigments, characterized since the early studies, have absorbance maxima ranging from the ultraviolet into the red. From this more recent work it followed that the Dartnall nomogram was only appropriate for visual pigments with a maximal absorbance at about 500 nm, i.e. in the blue-green. Visual pigments peaking in either the longer- or the shorter-wavelength range exhibited systematic deviations (e.g. Liebman, 1972). Therefore, Ebrey and Honig (1977) constructed improved nomograms to be applied in three wavelength ranges, i.e. the short-, middle- and long-wavelength range, respectively, for both vitamin A_1- and vitamin A_2-based visual pigments. Subsequently, Metzler and Harris (1978) reported an analytical expression derived from the lognormal function (see Appendix), which well fitted experimental absorbance spectra. Dawis (1981) approximated log absorbance curves with a polynomial expression (of the 8th degree), with different parameters for the three wavelength ranges.

An invariant shape was regained by Barlow (1982) by plotting the spectra as a function of $\lambda^{1/4} - \lambda_{max}^{1/4}$. Tabulated data for constructing the absorbance spectrum of any A_1-based visual pigment from λ_{max} using the Barlow transform can be found in Dartnall, Bowmaker and Mollon (1983). An analytical expression based on the Barlow transform has been given by Maksimov (1988).

An alternative invariant shape has been deduced by Mansfield (1985) and MacNichol (1986). These authors showed that plotting the experimental spectra at a frequency scale relative to the peak frequency, i.e. $f/f_{max} = \lambda_{max}/\lambda$, transforms both vitamin A_1- and vitamin A_2-based visual pigments into a unique shape. This conclusion is supported by Bowmaker, Astell, Hunt and Mollon (1991) who confirmed MacNichol, Jones, Cornwall and Mansfield (1987) in that the Mansfield–MacNichol (MM) transform, compared to the Barlow transform (slightly) better approximates an invariant shape of experimentally measured absorbance spectra. The MM transform has an intrinsic elegance in that the spectral shape is also constant when plotted as a function of log wavelength, or, equivalently, as a function of log wavenumber. By shifting along a log wavelength scale, Schnapf, Kraft, Nunn and Baylor (1988) could simply demonstrate that the sensitivity

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spectra obtained from photocurrent measurements on isolated cone cells have an identical shape over many log units of sensitivity (see also e.g. Baylor, 1987). The rod cell's spectral slope seems to differ very slightly at longer wavelengths, however (see also Mansfield, Levine, Lipetz, Olcszko-Szuts & MacNichol, 1986).

The value of describing visual pigment spectra with templates can be appreciated from the study of Lipetz and Cronin (1988), for example, who applied the MM transform to measured absorbance spectra of a number of crustaceans. By comparing predictions from the A_1- and A_2-templates they found that only the A_1-template matched well and thus concluded that the investigated crustacean visual pigments had retinal as chromophore.

Recently, Partridge and De Grip (1991) constructed a new template for vitamin A_1-based visual pigments from the absorbance spectrum of purified bovine rhodopsin. Applying the MM transform they derived a cubic polynomial fitting the long wavelength limb as well as a Chebyshev polynomial modelling the whole template accurately. The authors illustrate the validity of their standard curve on measured absorbance spectra of various fish visual pigments.

Bands in visual pigment spectra

We recall here that the main absorbance band of visual pigments is coined the α-band. Bovine rhodopsin, for example, has a main, broad α-band at about 500 nm; a low, broad β-band at about 350 nm, which is due to the *cis*-band of the chromophore; a narrow γ-band at 280 nm, which is due to certain amino acids of the protein part; a δ-band at 231 nm, which is due to a variety of organic bonds (review: Rodieck, 1973); and so on, see e.g. Stavenga and Van Barneveld (1975).

Virtually all approaches describing the shape of visual pigment spectra by means of a template or an analytical expression have been essentially restricted to the α-band. This invariably causes deviations at the shorter wavelengths, i.e. in the violet, because the β-band starts to cut in there. Actually, as argued in the Discussion, this effect underlies the less satisfactory Barlow transform.

In most vertebrate cases the β-band is considered to be of little importance because of ultraviolet blockage by the dioptric apparatus. Nevertheless, in many invertebrate eyes the ultraviolet range is of prime importance. Spectral sensitivity measurements of insect photoreceptors indicate that sensitivity becomes very low at wavelengths below 300 nm. This finding is in accordance with measurements of the photosensitivity of bovine rhodopsin, that also drastically decreases in the far-ultraviolet (see Dartnall, 1972, Fig. 3). Photosensitivity is the product of the molecular absorbance coefficient and the photoconversion quantum efficiency (Dartnall, 1972; Stavenga & Schwemer, 1984). For bovine rhodopsin, absorbance and photosensitivity appear to have a constant ratio at wavelengths above ≈ 300 nm. The quantum efficiency hence appears to be constant for the range of the α- and β-bands. Therefore, templates and analytical expressions can be applied to both absorbance spectra and physiologically measured spectral sensitivities. The quantum efficiency evidently is small in the range of the γ, δ, etc. bands. This means that only the α- and β-bands are due to absorption by the chromophore and that this induces photoisomerization and phototransduction.*

Metzler and co-workers analysed the absorbance spectra of several organic compounds and thus found that the spectra could be well described by algebraically adding lognormally shaped absorbance bands (e.g. Siano & Metzler, 1969; Metzler & Harris, 1978; Metzler, Cahill & Metzler, 1980; Metzler, Cahill, Petty, Metzler & Lang, 1985). This approach was also successfully applied to a few visual pigments by Metzler and Harris (1978). However, their lognormal function breaks down at the longer wavelengths (see Appendix), and hence another formalism has to be used there. In the so-called long-wavelength tail, experimentally measured log sensitivities become linearly dependent on frequency. Lewis (1955) presented a theoretical treatment of the absorbance spectrum of visual pigments in the long wavelength range (see also e.g. Vos & Van Norren, 1984). Mooij and Van den Berg (1983) incorporated this theory in their study of the spectral shape of A_2 visual pigments. They fitted the absorbance bands of measured visual pigment spectra with Metzler-type lognormal curves, but used a Lewis function for the long wavelength region.

In the present paper we continue this type of analysis by assuming that the MM transform holds for the α-band irrespective of the spectral position of the band. Furthermore, we assume that, relative to the α-band, the β- and γ-bands are more or less constant with respect to both spectral location, shape and amplitude, at least for visual pigments with the same type of chromophore (see e.g. Wald, Brown & Smith, 1955; Menzel, Ventura, Hertel, De Souza & Greggers, 1986; Kirschfeld, 1986). Here we present simple analytical expressions as well as parameter values yielding satisfactory fits to experimental spectra, together with related results following for the Metzler lognormal function.

RESULTS

The spectral shape of the α-band

Generally, spectral absorbance bands of condensed matter have a Gaussian shape when plotted as a function of frequency, or, the log absorbance curve then is a parabola. The absorbance bands of visual pigments, rather than simple Gaussians are skewed toward higher energies (Metzler & Harris, 1978). Partridge and De Grip (1991) reported a highly accurate, normalized spectrum of bovine rhodopsin. In Fig. 1(a) we have

*We have to note here that the fly eye makes an exception to this well-established concept. The spectral sensitivity of fly photoreceptor cells can be considerably enhanced in the ultraviolet due to an ultraviolet-absorbing, sensitizing pigment. Devoid of the sensitizer the spectral sensitivity has a normal, low β-peak (review, Kirschfeld, 1986; Vogt, 1988; Hamdorf *et al.*, 1992). Furthermore, we note that some energy transfer by the protein to the chromophore may occur.

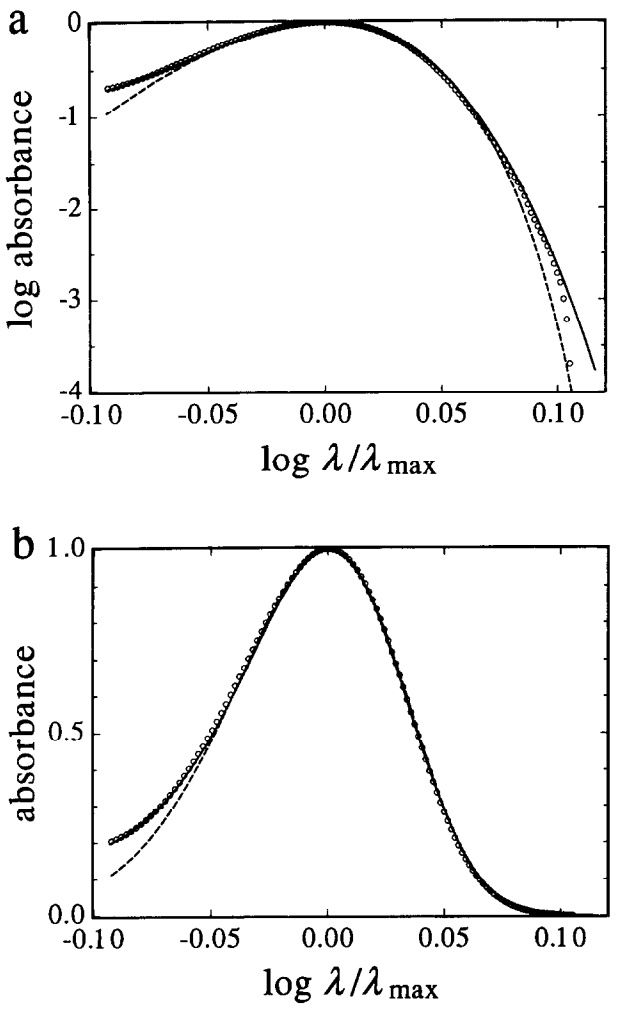

FIGURE 1. Normalized absorbance spectrum of bovine rhodopsin, tabulated by Partridge and De Grip (1991), symbols, fitted with the modified lognormal function, equation (1) (continuous line) and the Metzler function, equation (A1–A3) (interrupted curve). (a) The logarithm of the absorbance is taken to assess the Gaussian-like shape of the absorbance curves. (b) The same data at a linear ordinate scale showing the excellent fit.

plotted the logarithm of the tabulated absorbance values as a function of log wavelength. A modified lognormal function with no more than a third degree term in the exponent appears to fit the data quite well:

$$\alpha = A \exp[-a_0 x^2(1 + a_1 x)]. \quad (1)$$

Here $x = {}^{10}\log(\lambda/\lambda_{max})$, with $A = 1.006$, $\lambda_{max} = 497.4$ nm, and $a_0 = 393$ and $a_1 = 5.65$ [Fig. 1(b)]. With the restriction that $A = 1.000$, it follows that $\lambda_{max} = 497.4$ nm, $a_0 = 389$, $a_1 = 5.60$. At any data point the maximal deviation is $< 1\%$ of the maximal absorbance (Fig. 2).

The parameter x equals the log of the relative wavelength, or, minus the log of the relative frequency. The deduced fit therefore can immediately be used for calculating the absorbance spectrum of any visual pigment given its peak wavelength λ_{max}, assuming of course the validity of the MM transform.

We have fitted the Partridge and De Grip data also with a Metzler-type lognormal function (see Appendix). Figure 1(b) demonstrates that this function yields a good fit for parameter values $\lambda_{max} = 497.0$ nm, relative bandwidth $W/f_{max} = 0.203$ and skewness $\rho = 1.37$ (for similar values, see Metzler & Harris, 1978). Fit and experimental data deviate at the shorter wavelengths, but, as described below, this is readily accounted for by an additional band (see Metzler & Harris, 1978).

The β-band

A major shortcoming of equation (1) emerges when it is extrapolated into the short-wavelength range. The third-degree term then becomes dominant and the calculated absorbance value has no upper bound. This can be simply resolved by introducing a fourth-degree term into the exponent of equation (1). When we assume that all absorbance bands are described by the same modified lognormal function, or,

$$\alpha_i = A_i \exp[-a_{0i} x_i^2(1 + a_{1,i} x_i + a_{2,i} x_i^2)] \quad (2)$$

with $i = \alpha$, β, ... etc., and $x_\alpha = {}^{10}\log(\lambda/\lambda_{max,\alpha})$, $x_\beta = {}^{10}\log(\lambda/\lambda_{max,\beta})$, etc., with $\lambda_{max,\alpha}$, $\lambda_{max,\beta}$, ... etc. the peak wavelengths of the α-, β-, ... etc. bands. We then obtain for the visual pigment spectrum:

$$\epsilon(\lambda) = \Sigma\alpha_i(\lambda) = \alpha(\lambda) + \beta(\lambda) + \gamma(\lambda) + \ldots \quad (3)$$

We have restricted the parametrization, however, by requiring that $a_{2,i} = 3a_{1,i}^2/8$; the log absorbance of each band, i.e. the polynomial in the exponent, then has only one inflection point.

We have tested the validity of equation (3) on a complete absorbance spectrum of bovine rhodopsin, taken from Morton (1972, Fig. 4). In our fits we have used the values of the shape parameters of the α-band, $a_{0,\alpha} a_{1,\alpha}$ (and $a_{2,\alpha}$), that well fitted the Partridge and De Grip (1991) data; $\lambda_{max,\alpha}$ was a free parameter, however. Figure 3 shows the data points as well as the fit, normalized at the α-peak. The parameter values obtained from fitting equations (2) and (3) as well as those from fitting the Metzler function (Appendix) are listed in

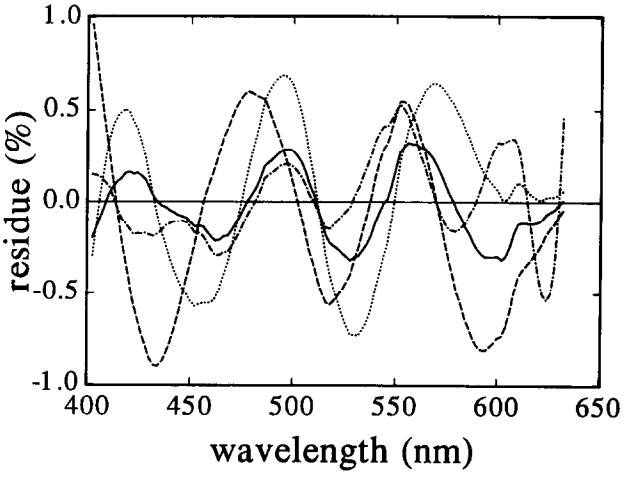

FIGURE 2. Deviations of tabulated data of Partridge and De Grip (1991) and fits. Dot-dashed line, difference with 10th degree Chebyshev polynomial fit using the values given by Partridge and De Grip (1991); dashed line, difference with fit with Metzler-lognormal curves; dotted line, difference with values of equation (1); solid line, difference with values predicted by equation (2). Fitting was performed on the linear (scaled) absorbance values with the Gauss–Newton least-square curve fitting algorithm, as implemented in the high level language ASYST (MacMillan Software Company).

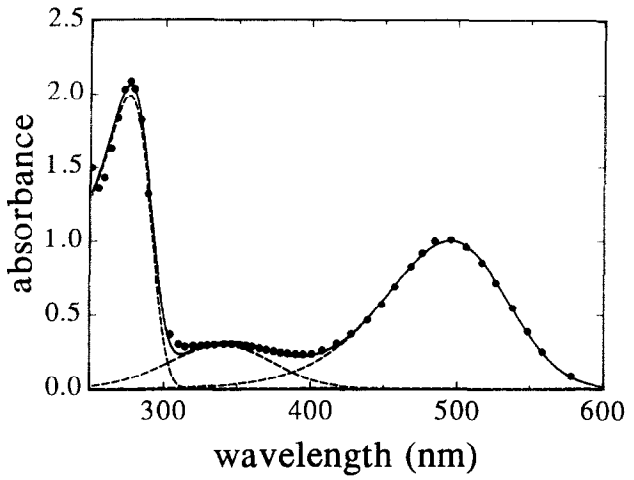

FIGURE 3. Absorbance spectrum of bovine rhodopsin, normalized at the α-peak (Morton, 1972, Fig. 4). The dashed lines represent the absorbances of the α-, β- and γ-band, following from fitting equations (2) and (3) to the complete spectrum.

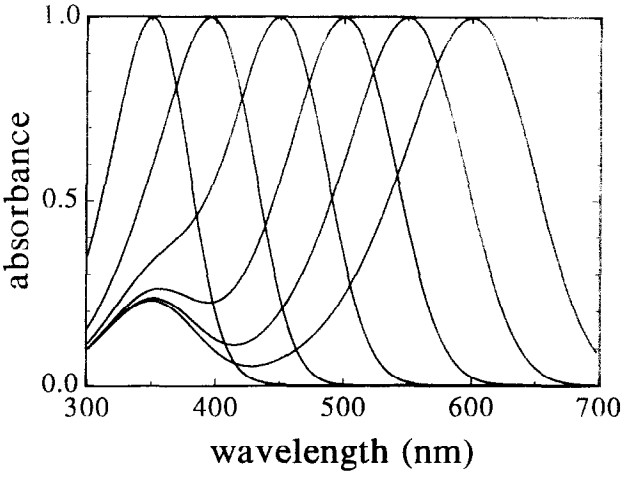

FIGURE 4. Normalized absorbance spectra predicted by equations (2) and (3) for $\lambda_{max,\alpha} = 350$, 400, 450, 500, 550 and 600 nm using for the other parameters values deduced for bovine rhodopsin. The β-band becomes distinctly noticeable when $\lambda_{max,\alpha} \geq 450$ nm.

Table 1. We note here that the magnitude of the β-band in Fig. 3, $A_\beta = 0.29$ is distinctly higher than that of more recently published spectra (e.g. De Grip, Daemen & Bonting, 1980), where $A_\beta = 0.23$.

It appears that the accuracy of the obtained fits is virtually identical to that obtained with the 10th degree Chebyshev polynomial, as presented by Partridge and De Grip (1991), see Fig. 2. The deviations of the fits from the experimental data, being at most 0.5%, appear as systematic oscillations. Possibly, these are due to the vibrational fine structure of the absorbance band (see e.g. Metzler *et al.*, 1985).

Predictions

Apparently, the β-band contributes significantly in the short wavelength range up to about 440 nm (Fig. 3). The effect of adding the absorbances of the α- and β-bands is exemplified in Fig. 4. Using the derived parameter values, we have calculated the normalized absorbance spectrum of six visual pigments with $\lambda_{max,\alpha} = 350$–600 nm. For the β-band we have taken a fixed $\lambda_{max,\beta} = 350$ nm. Clearly, the β-band becomes more and more distinct when $\lambda_{max,\alpha} \geq 450$ nm.

The long-wavelength tail

It is evident from Fig. 1(a) that the absorbance values tabulated by Partridge and De Grip (1991) go too fast towards zero for wavelengths above 620 nm, i.e. where the normalized absorbance decreases below 0.3%. Although we regard this part of the data as unrealistic, the Partridge and De Grip (1991) data presumably are the best presently available. The two functions used to fit the absorbance data both become unsatisfactory at the longer wavelengths. Obviously, the Metzler function falls off too steep, but it appears that also the modified lognormal functions of equations (1) and (2) do not qualify.

Because the absorbance in the far-red is very minor it can only be reliably determined there via sensitivity measurements, assuming a constant quantum efficiency

TABLE 1. Parameter values for A_1-, A_2-, and A_4-visual pigments for exponential expressions equation (2) (SSH) and equation (A1) (MH), respectively

	SSH	α	β	γ	MH	α	β	γ
A_1	λ_{max}	495.3	340	276	λ_{max}	494.7	340	275
	A	1	0.29	1.99	A	1	0.30	1.94
	a_0	380	247	647	W/f_{max}	0.203	0.32	0.156
	a_1	6.09	3.59	23.4	ρ	1.37	1.4	1.64
A_2	λ_{max}	534.3	368	—	λ_{max}	533.3	368	
	A	1	0.50	—	A	1	0.52	
	a_0	263	176	—	W/f_{max}	0.254	0.24	—
	a_1	4.45	1.52	—	ρ	1.44	1.4	—
A_4	λ_{max}	485.8	329	277	λ_{max}	485.4	331	276
	A	1	0.23	1.59	A	1	0.25	1.55
	a_0	420	252	894	W/f_{max}	0.197	0.31	0.145
	a_1	7.73	2.97	19.5	ρ	1.46	1.3	1.67

λ_{max} in nm and $a_2 = 3a_1^2/8$ in equation (2). The data of Partridge and De Grip (1991) yielded the shape parameters for the A_1-visual pigment ($a_{0,\alpha}$ and $a_{1,\alpha}$, and W/f_{max} and ρ, respectively), but the other parameters were obtained for the complete spectrum of Morton (1972, Fig. 4). The data for the A_2-visual pigment were derived from the porphyropsin spectrum of Bridges (1972, Fig. 6) and that for the A_4-visual pigment from the data tabulated by Kito *et al.* (1992).

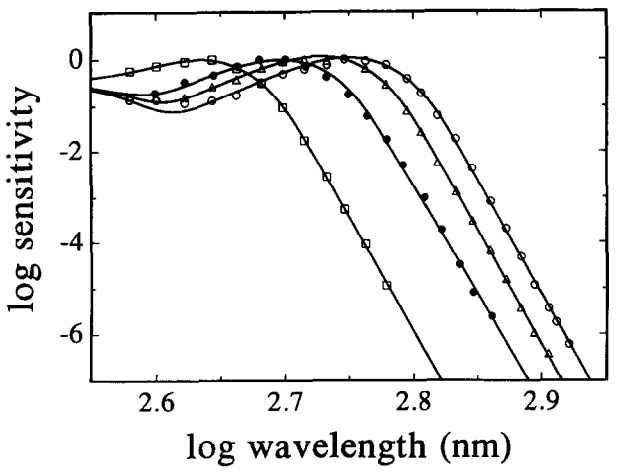

FIGURE 5. Spectral sensitivities of primate photoreceptors, determined by measuring photocurrents (Schnapf *et al.*, 1988), together with curves calculated from equation (2), extended with a log-linear function in the long wavelength range (see text).

(see Introduction). The electrophysiologically measured sensitivity spectra of primate photoreceptors decrease approximately log linearly, i.e. with a first-degree exponential, at a log wavenumber scale (Schnapf, Kraft & Baylor, 1987; Baylor, Nunn & Schnapf, 1987; Schnapf *et al.*, 1988; for a corresponding invertebrate case, viz. *Limulus*, see Srebro, 1966). The long-wavelength tail of the spectra hence is not well described by equations (1) and (2). It appears that these equations can only be applied up to $^{10}\log(\lambda/\lambda_{\max,\alpha}) \approx 0.1$.

Figure 5 shows the fits to the results of Schnapf *et al.* (1988), where in the case of the cone curves the logarithm of equation (2) was used up to $x_\alpha = {}^{10}\log(\lambda/\lambda_{\max,\alpha}) = 0.080$; for the rod this value was 0.078. Above these values the log sensitivity is well approximated by a linear function $\log S = s(x_\alpha - x_0)$, with slope $s = -50.9$ and $x_0 = 0.047$ (cones) and $s = -48.2$ and $x_0 = 0.046$ (rod), respectively (see Baylor, 1987). We note that Baylor *et al.* (1987) approximated their complete spectra, including the long-wavelength tail, with a sixth order polynomial.

Vitamin A_2-based visual pigments

The spectral shape of rhodopsins, i.e. the vitamin A_1-based visual pigments, differs from that of the porphyropsins, i.e. the vitamin A_2-based visual pigments. Assuming that the MM transform also holds for this visual pigment class (MacNichol, 1986), we have fitted both equations (2) and (3) and the Metzler function to the porphyropsin curve of Bridges (1972, Fig. 6). The deduced parameters are summarized in Table 1.

Vitamin A_3-based visual pigments

A_3-visual pigments, where the chromophore is 3-hydroxyretinal, are found in the higher insects, specifically flies (Kirschfeld, 1986; Vogt, 1988). The absorbance spectra obtained indicate that the α-band not appreciably differs from that of the A_1-visual pigments (see e.g. Schwemer, 1988). Therefore, the parameters deduced for bovine rhodopsin should be used in this case. A formal description of the short-wavelength range is cumbersome, because the relative height as well as the band shape in the ultraviolet strongly depends on the amount of sensitizing pigment (Kirschfeld, 1986; Hamdorf, Hochstrasse, Höglund, Moser, Sperber & Schlecht, 1992); see footnote on p. 1012.

Vitamin A_4-based visual pigments

The only animal known to possess an A_4-visual pigment, where the chromophore is 4-hydroxyretinal, is the firefly squid *Watesina scintillans* (Matsui, Seidou, Uchiyama, Sekiya, Hiraki, Yoshihara & Kito, 1988). (It has in addition an A_1- and an A_2-visual pigment.) Recently, Kito, Partridge, Seidou, Narita, Hamanaka, Michinomae, Sekiya and Yoshihara (1992) provided tabulated absorbance data of the extracted A_4-visual pigment. These authors, furthermore, constructed a synthetic pigment from bovine opsin and 4-hydroxyretinal. The spectral shapes of the two A_4-pigments appeared to be very similar, as followed from polynomial fits, and differed noticeably from that of bovine rhodopsin.

We have fitted the tabulated data with equations (2) and (3) as well as with the Metzler function and thus derived the parameters for the A_4-visual pigment, assuming again that the MM transform holds; see Table 1.

DISCUSSION

Starting from an accurately measured absorbance spectrum of bovine rhodopsin we have derived expressions for the spectral shape of any visual pigment spectrum, given the peak wavelength. We have assumed the validity of the MM transform, i.e. that the shape is constant at a $\lambda/\lambda_{\max}$-axis, or, at a log λ-axis. Figure 6 shows that more or less different spectra are predicted by the transforms proposed by Dartnall, i.e. a constant shape at a $1/\lambda$-axis, and by Barlow, i.e. a constant shape at a $\lambda^{1/4}$-axis. It appears that results of the MM and

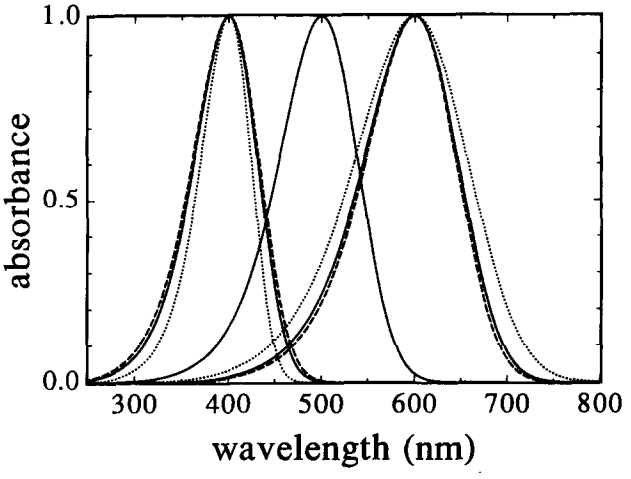

FIGURE 6. Comparison of three visual pigment transforms for rhodopsin α-bands. The same template was used, given by the α-band peaking at 500 nm and calculated with equation (2). The spectra predicted by the Dartnall (dots), Barlow (interrupted line) and MM (continuous line) transforms are given for peak wavelengths 400 and 600 nm, respectively.

Barlow transforms are rather similar indeed. Interestingly, Barlow (1982) investigated the validity of the log λ-transform. He rejected it after comparing the bandwidths of experimental absorbance spectra of red and blue photoreceptor pigments. The bandwidth was measured from the peak wavelength to the 50% absorbance point on the long wavelength side. At the log λ-axis, the absorbance spectrum of the blue pigment, peaking at 416 nm, was distinctly wider than that of the red pigment, peaking at 567 nm, whilst at a λ^{-1}-axis the width was concluded to be identical. However, it follows from our analysis that Barlow's estimation is possibly fraught with a critical error. Figure 5 shows that the peak wavelength, λ_{max}, of a blue pigment is affected by the β-band. Its value is shifted hypsochromically with respect to that of the α-band alone. When the peak wavelength of the total spectrum is 416 nm, the α-band will peak at approx. 419 nm. Then the bandwidth calculated for the α-band becomes virtually identical to that of the red pigment (which does not suffer from the contaminating effect of the overlapping bands).

The parameter values to be used for the α-band in equation (1)–(3) for vitamin A_1-based visual pigments are derived from the tabulated spectrum of Partridge and De Grip (1991). Future studies may refine the experimental data, so the parameters are subject to a slight change. We assume that a much higher accuracy can hardly be expected, however, and therefore we feel that the derived expressions and parameter values will not be much improved. We note that in applications to experimental data equation (1) is especially simple. We have abstained from giving an estimate of confidence. For any practical purpose, varying the value of most parameters with a few percent gave equally well-fitting spectra. Compared to the Chebyshev polynomial proposed by Partridge and De Grip (1991), equations (1) and (2) are much easier implemented in any computer program or worksheet. As stated in the Appendix, the Metzler function is also quite attractive.

Usually, only the α-band is of direct interest. For instance, in the case of most vertebrate eyes the lens absorption severely affects the measurements in the short-wavelength range (see Schnapf *et al.*, 1988). An absorbance spectrum of a visual pigment, spanning the range of several bands, can be usefully described by equations (2) and (3). This will be especially beneficial in electrophysiological or behavioural studies of spectral sensitivity. We emphasize that in both equations (1) and (2), as in the Metzler function, no more than two free variables were used to fit the shape of each band.

The family of curves of Fig. 5 exhibit a striking resemblance to spectra in the literature, for instance of iodopsin (Wald *et al.*, 1955) or the three photoreceptors of the honeybee (Menzel *et al.*, 1986). Unfortunately, however, a quantitative comparison indicates that the experimental data probably are not identical to pure absorbance spectra of visual pigments, either due to contaminations by other absorbing components, or, in the case of electrophysiological measurements, due to the inevitable optical effects of waveguides, stray light or optical filtering. Nevertheless, from the scarce and, presumably, not always very solid data in the literature the impression emerges that the β-peak wavelength can vary between 330 and 360 nm and that the magnitude of the β-peak, relative to that of the α-peak, also somewhat varies. The slight uncertainty in the β-band will have a minor effect on the overall appearance of the absorbance spectrum of a visual pigment, however.

A major point of this paper is that a complete visual pigment spectrum can be resolved in several bands. Estimation of their precise location and shape will be facilitated by fitting first the α-band and subsequently the β-band. The bands can be fitted appropriately with lognormal functions. The long wavelength range should be treated separately (cf. Baylor *et al.*, 1987). The spectra of Van Dijk and Spekreijse (1984) suggest that also in the case of A_2-visual pigments not only the main absorbance bands, but also the long wavelength tail is MM invariant. More accurate measurements of this aspect and of visual pigment spectra in general are necessary to refine the present description.

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Acknowledgements—J. H. van Hateren and J. Schwemer read the manuscript. We thank an unknown referee for important criticism. This research has been supported by the Netherlands Organization for Pure Research (N.W.O.) through the Foundation for Biophysics.

APPENDIX

The lognormal function provided by Metzler and Harris (1978) that describes the shape of absorbance bands of organic substances, including visual pigments, is:

$$\alpha(f) = A \exp -\frac{\ln 2}{(\ln\rho)^2}\left[\ln\left(\frac{f_{\max}}{W}\left(\rho - \frac{1}{\rho}\right)\left(\frac{f}{f_{\max}} - 1\right) + 1\right)\right]^2 \quad \text{(A1)}$$

when

$$\frac{f}{f_{\max}} > 1 - \frac{W}{f_{\max}}\left[\rho - \frac{1}{\rho}\right]^{-1} \quad \text{(A2)}$$

and

$$\alpha(f) = 0; \quad \frac{f}{f_{\max}} < 1 - \frac{W}{f_{\max}}\left[\rho - \frac{1}{\rho}\right]^{-1}. \quad \text{(A3)}$$

Here f is the frequency (or, equivalently, the wavenumber), $f_{\max}$ the frequency of the peak, W the width at half height, and ρ the skewness of the band; i.e. if f_v and f_r are the frequencies of the half maximal values at the violet and red end, respectively, then: $W = f_v - f_r$ and $\rho = (f_v - f_{\max})/(f_{\max} - f_r)$ (see also Siano & Metzler, 1969). The Metzler lognormal function thus has intrinsic attractive properties, because it incorporates quantities that are directly measurable from a spectrum. However, it has found so far very little use in the visual literature (see nevertheless, e.g. Birge, 1990). Because $f/f_{\max} = \lambda_{\max}/\lambda$ it is clear that the parameter values derived by Metzler and Harris (1978) for rhodopsin and porphyropsin can be applied to related visual pigments by using the MM transform. Note that the lognormal curve is breaking down in the long-wavelength range, where the absorbance is assumed to become zero.